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KRISTA TAKKIS

Changes in plant species richness and population performance in response to habitat loss and fragmentation

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Changes in plant species richness and population performance in response to habitat loss and fragmentation

UNIVERSITY OF TARTU
PRESS
1632

Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in botany and mycology at the University of Tartu on February 17, 2014 by the Scientific Council of the Institute of Ecology and Earth Sciences University of Tartu.

Supervisors: Prof. Meelis Pärtel and Dr. Aveliina Helm, University of Tartu, Estonia

Opponent: Prof. Markus Fischer, University of Bern, Switzerland

Commencement: Room 218, 40 Lai Street, Tartu, on May 12, 2014 at 10.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu and by the Doctoral School of Earth Sciences and Ecology created under the auspices of European Social Fund.

ISSN 1024–6479
ISBN 978–9949–32–518–4 (print)
ISBN 978–9949–32–519–1 (pdf)

University of Tartu Press
www.tyk.ee

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which are denoted in the text by the Roman numerals:

I Helm, A., Oja, T., Saar, L., Takkis, K., Talve, T. & Pärtel, M. 2009. Human influence lowers plant genetic diversity in communities with extinction debt. *Journal of Ecology* 97: 1329–1336

II Takkis, K., Pärtel, M., Saar, L. & Helm, A. 2013. Extinction debt in a common grassland species: immediate and delayed responses of plant and population fitness. *Plant Ecology* 214: 953–963

III Saar, L., Takkis, K., Pärtel, M. & Helm, A. 2012. Which plant traits predict species loss in calcareous grasslands with extinction debt? *Diversity and Distributions* 18: 808–817

IV Takkis, K., Saar, L., Pärtel, M. & Helm, A. The role of environmental and landscape factors in determining plant abundance and fitness-related traits in six specialist plant species in fragmented grasslands. *Manuscript*

Author's contribution to the publications:

I participated in data collection and manuscript preparation
II had the main responsibility in developing the idea, designing the methodology, collecting and analysing the data and preparing the manuscript
III participated in data collection and manuscript preparation
IV had the main responsibility in developing the idea, designing the methodology, collecting and analysing the data and preparing the manuscript

1. INTRODUCTION

1.1. Theoretical background

Human induced habitat loss and fragmentation are one of the greatest biodiversity hazards today, threatening communities with an impending loss of habitat specialist species (Balmford et al. 2005; Krauss et al. 2010; Pereira et al. 2012). Decreasing and more isolated habitats often harbour smaller populations with reduced genetic diversity, higher inbreeding and increased susceptibility to stochastic environmental and population dynamic events (Matthies et al. 2004; Leimu et al. 2006). Several studies have recorded specialist plant species that have gone locally extinct or have rapidly declined due to habitat loss and degradation within a period of a few decades or centuries (Fischer & Stöcklin 1997; Walker & Preston 2006; Wesche et al. 2012). At the same time, communities can exhibit a delay in species loss due to slow intrinsic dynamics of populations (Hanski & Ovaskainen 2002). This phenomenon, called extinction debt, can mask the imminent species disappearance for decades or even centuries after the initial landscape changes and disguise the need for urgent conservation measures (Vellend et al. 2006; Kuussaari et al. 2009).

Life-history traits can determine a species vulnerability to changes in landscape configuration and environmental conditions (Fischer & Stöcklin 1997; Lindborg et al. 2012; Marini et al. 2012). Traits related to dispersal ability and persistence capability are particularly important in fragmented and degraded habitats (Kolb & Diekmann 2005; Tremlová & Münzbergová 2007). Species with good dispersal ability are generally considered to be less susceptible to habitat fragmentation (Ozinga et al. 2004). However, when the connectivity of habitat patches decreases further, dispersal related mortality can become higher and good dispersers may eventually become disadvantaged (Murphy & Lovett-Doust 2004; Riba et al. 2009). In strongly isolated and degraded habitats, better persistence and competitive abilities can become beneficial and species with longer life span, clonal propagation and persistent seed bank can be more successful than good dispersers (Maurer et al. 2003; Piqueray et al. 2011). In contrast, Lindborg et al. (2012) and Marini et al. (2012) demonstrated a decrease in the number of long-lived and clonal species with decreasing habitat area and argued this to be a result of long-term changes in landscape structure and local processes.

Plant populations respond to habitat loss and fragmentation with a time-lag, thus eventually giving rise to the extinction debt observed in species richness at remnant sites (Ewers & Didham 2006; Hylander & Ehrlén 2013). Due to long generation times, clonal growth and slow intrinsic population dynamics, the effect of landscape changes on plant and population fitness can manifest with a delay, making it more difficult to evaluate population condition in remnant habitats (Ewers & Didham 2006). Delayed responses to landscape changes can indicate poor adaptation capability and possibly a greater likelihood of future population decline. At the same time, the strong association between current

landscape structure and population fitness can signify rapid response and possible adaptation to habitat changes, although this relationship can also indicate a future threat in case of continuing habitat loss and fragmentation. Many studies have previously observed trait responses to habitat changes, finding highly ambiguous results depending on species life-history traits and characteristics of the study system (e.g. Hooftman et al. 2003; Kolb and Lindhorst 2006; Winter et al. 2008; Leimu 2010), thus indicating the need for further in-depth research accounting for habitat history, time-lagged responses of species populations (Hylander & Ehrlén 2013) and other confounding factors that can influence the attained results (Ewers & Didham 2006).

One of the main reasons for the detrimental effect of habitat loss and increasing isolation on population fitness in remnant habitats is the disrupted gene flow, which can decrease the genetic diversity and increase inbreeding effects (Lienert 2004; Ouborg et al. 2006; Aguilar et al. 2008). The genetic deterioration of populations can hinder plant evolutionary potential and ability to adapt to changes in the environment (Ouborg et al. 2006). The genetic diversity forms over a long time and, similarly to species richness, is affected by many landscape-scale processes, like long-term conditions for seed and pollen dispersal (Vellend 2004; Vellend & Geber 2005). At the same time, genetic diversity can be more sensitive to changes in these processes than species richness and is often the first level of biodiversity which reveals the effects of habitat loss (Lienert 2004; Aguilar et al. 2008). Therefore it is essential to integrate population genetic information into population fitness and landscape ecological studies to ensure insightful results and the use of proper measures in conservation programs (Ouborg et al. 2006; Picó & Van Groenendael 2007).

European semi-natural grasslands have gone through extensive area loss over the last centuries. Most former semi-natural grasslands in Europe are now intensively managed, afforested or overgrown with trees and shrubs due to the cessation of traditional management, land-use changes and eutrophication (Poschlod & WallisDeVries 2002; Pärtel et al. 2005). Lower habitat quality in remnant grasslands can impair the probability of persistence of species more vulnerable to these changes (Fischer & Stöcklin 1997). For example, Estonian dry calcareous and shallow-soiled grasslands (alvars) have lost more than 70% of their former area over the last century. An extinction debt of 40% has been found at the more stable grasslands, whereas the unstable habitats, which have lost most of their historical area, have already lost a large part of their former species richness (Helm et al. 2006). Consequently, considerable changes in species diversity and population fitness of the species forming the extinction debt can be anticipated in these grasslands in course of time. Raising our awareness of the expected changes and their causes can help us prevent or at least hinder the loss of genetic diversity, population fitness and species richness in these grasslands by augmenting the conditions supporting species persistence in semi-natural grasslands.

1.2. Objectives of the thesis

The main goal of this thesis was to study the effects of habitat loss and fragmentation on species diversity and population performance from the perspective of genetic diversity, species life-history traits and plant trait responses using Estonian semi-natural alvar grasslands as a model system. First, we studied the genetic diversity and population fitness of a grassland specialist grass species *Briza media* L. in relation to current and historical landscape configuration and local environmental conditions in papers **I** and **II**. Second, we further expanded the study, examining the local extinctions on a community level and testing for dissimilar responses in species with different susceptibility to land-use changes in papers **III** and **IV**.

We studied the grassland specialist *B. media* in alvar grasslands in western Estonia. A long-term human influence on species richness in these grasslands has been previously demonstrated (Pärtel et al. 2007), as have the subsequent changes in the system following land-use change and cessation of traditional management over the last century (Pärtel et al. 2005), including an extinction debt in the grassland plant communities (Helm et al. 2006). We examined the effect of landscape changes and human population density on the genetic diversity of *B. media* (**I**), additionally including local environmental conditions in the study of *B. media* population performance (**II**) in order to distinguish the most important factors determining population fitness and the likelihood of persistence of *B. media* in the remnant habitat fragments. We combined the genetic, population and species diversity data to determine a possible time-lag in population performance response to landscape changes, which might affect our evaluation of population fitness from the conservational perspective.

Subsequently, we expanded our study to investigate the effect of landscape changes on the community level and on species with different life-histories. Most studies examining extinction debt use indirect estimates, relating current species richness to landscape structure in different timescales (Piessens & Hermy 2006; Lindborg 2007). Direct comparisons with historical species lists from particular locations can provide more information on specific species that have been lost, however good quality historical datasets are seldom available (Fischer & Stöcklin 1997; Kuussaari et al. 2009). In paper **III** we were able to compare historical species lists from the 1920s (Vilberg 1927) to current lists compiled at the same locations in northern Estonian alvars. We directly documented which species had been lost from the sites within 90 years of extensive land-use change, fragmentation and environmental degradation, and which traits and trait values characterised the declining or locally extinct species. This knowledge can imply which species are potentially more susceptible to changes in the less altered semi-natural grasslands where these species are still present.

Unlike the northern Estonian grasslands, the alvars in western Estonia have been subjected to comparatively milder changes and several species that are already locally extinct in northern Estonia are still present in the grasslands of western Estonia. However, an extinction debt has been revealed on the western

Estonian grasslands (Helm et al. 2006), indicating that at least some of the species will most likely be lost from these alvars sometime in the future. Prior to eventual extinction from local communities, species can exhibit a response to changes in habitat conditions, showing possible signs of local adaption or decreasing population fitness (Lienert 2004; Ewers & Didham 2006; Jacquemyn et al. 2012).)

In paper **IV** we explored the responses of six species with different life-history traits to land-use changes in western Estonian grasslands, using the results of paper **III** for species selection. Three phylogenetically related species pairs were selected, with one locally disappearing and one locally persistent species in northern Estonian alvars in each pair. We studied the responses of fitness-related traits to current and historical landscape structure, human influence and local environmental conditions to discern the most important factors determining population performance. We tested, whether there was a difference in the abundance and trait responses between the species more vulnerable and more resistant to land-use changes and environmental degradation in grasslands subjected to less severe changes.

Main objectives of the thesis were the following.

- To test, which landscape and local environmental parameters are most important in determining species local extinctions and population performance in fragmented grasslands (**I**–**IV**).
- To determine the influence of landscape changes on the genetic diversity of a specialist grass (**I**) and the effect of genetic diversity on plant and population traits in remnant habitats (**II**).
- To identify, which life-history traits and trait responses indicate higher susceptibility to landscape fragmentation in dry grassland species (**II**, **III** and **IV**).
- To test for a possible time-lag in the response of the genetic diversity and plant traits to landscape changes in grassland specialist species (**I**, **II** and **IV**).

2. MATERIALS AND METHODS

2.1. Study sites

All studies were conducted on alvar grasslands in two separate regions of Estonia (Fig. 1). Study **III** was conducted on 8 alvar grasslands in northern Estonia (ca 59° N, 24°–25° E), where an exhaustive vegetation analysis was performed in 1918–1923 (Vilberg 1927). For studies **I**, **II** and **IV**, a different set of alvars (34, 20 and 32 sites in papers **I**, **II** and **IV**, respectively) were sampled on the islands of Saaremaa and Muhu (ca 58° N, 22°–23° E), located in the Baltic Sea, west of the Estonian mainland (Fig. 1).

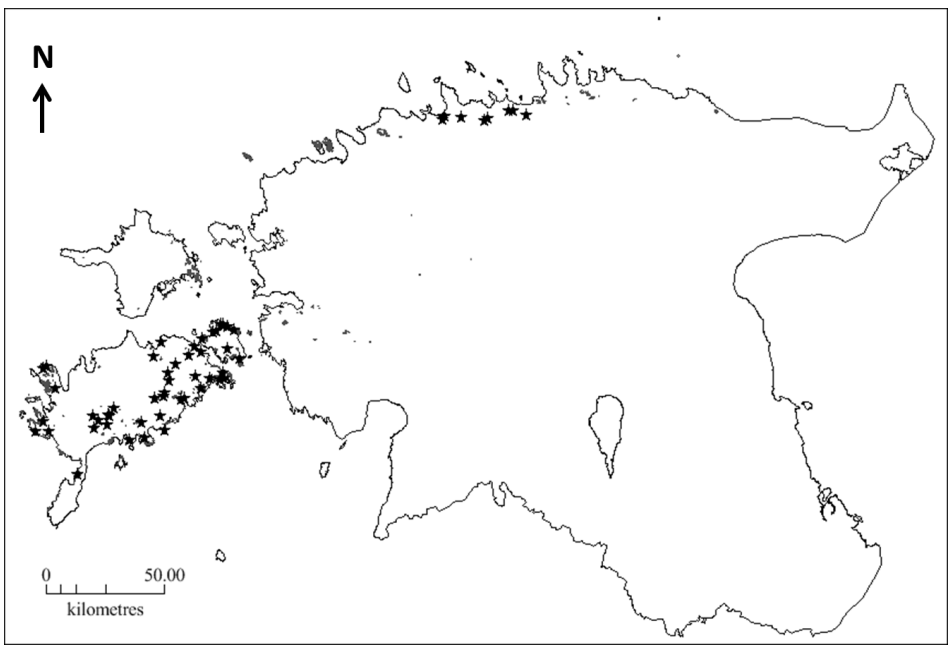

Figure 1. Study sites on alvar grasslands in western and northern Estonia are indicated with stars. Grey areas indicate alvar grasslands in Estonia in 2011 (Estonian Environmental Registry, data provided by the Estonian Environmental Board)

Alvar grasslands are dry calcareous semi-natural grasslands with shallow soil (< 20 cm), situated mostly in countries surrounding the Baltic Sea on Ordovician and Silurian limestone outcrops (Pärtel et al. 1999). These grasslands have developed over thousands of years due to continual human influence, most likely moderate grazing (Pärtel et al. 2007). In the beginning of the 20th century the traditional land-use patterns started changing. People left the smaller villages and new land-use techniques were introduced (Jänes-Kapp et al. 2007). After the Second World War, intensification of agriculture continued more

widely, followed by large afforestation campaigns on alvar grasslands in the 1960s and 1970s (Laasimer 1965; Jänes-Kapp et al. 2007). As a result of afforestation and cessation of traditional management, Estonian alvars have lost more than 70% of their area between the 1930s and the 2000s (Laasimer 1965; Helm et al. 2006). Alvars in northern Estonia have lost an even greater amount of their area (ca 90%; **I**) to intensive agriculture, quarries, road construction and expansion of Tallinn, the capital of Estonia. Alvars on the western Estonian islands are relatively better preserved and in spite of almost equally large habitat loss (more than 80%; **II**, **IV**), the environmental conditions on sites are in general less degraded and more favourable for alvar specialist species.

2.2. Study species and traits

2.2.1. Study species and measured plant and population traits

We used a common habitat specialist grass *Briza media* L. as a model species in studies **I** and **II**. *B. media* is a diploid (2n=14) perennial hemicryptophyte species growing in sparse tussocks (Dixon 2002). It is wind-pollinated and an obligatory cross-pollinator (Murray 1974). Diaspores are dispersed by wind, animals or hay (Dixon 2002; Prentice et al. 2006). *B. media* is considered an indicator of regularly managed high-quality grasslands with long management history (Prentice et al. 2006; Aavik et al. 2008).

Phenotypic and population performance of *B. media* (**II**) was evaluated by measuring plant height and counting the number of spikelets of 20 individuals per site as a proxy of plant potential reproductive output. The coefficient of variation (CV) of the number of spikelets was calculated to characterise the variation of potential reproductive output in populations. Population density of generative and non-flowering plants was obtained from 10 randomly placed 1×1 m sample plots, where all generative and non-flowering individuals were counted. In order to evaluate germination ability at different sites, seeds of *B. media* from 20 ramets per site were pooled and ~80 seeds were germinated per site on moist filter paper on room temperature. Germinated seeds were counted and the proportion of germinated seeds calculated for each site.

To test the relationships between trait responses and different landscape and environmental factors, three phylogenetically related alvar specialist species pairs were selected for study **IV** (see Table 2 in paper **IV**). Each pair consisted of one locally disappearing and one locally persistent species according to the study **III** in northern Estonian alvars in order to compare the responses of species groups under different local conditions. On the less degraded western Estonian alvars all six species are still present and relatively common.

To characterise the small-scale changes in population performance on remnant sites, the small-scale abundance of the six species (**IV**) was estimated on a 0.1×10 m transect as a proportion of presence/absence in each of the hundred 10×10 cm plots along the transect. Plant phenotypic performance was assessed by measuring plant height and gathering 15 randomly selected generative

ramets of each species per site. Dry biomass of plant vegetative and generative organs was weighed and plant reproductive allocation was calculated (generative/vegetative biomass). CV of plant height and reproductive allocation were additionally calculated to characterise the trait variation within a population.

2.2.2. Species richness and species extinction coefficient

We used previously collected (in 2001) species composition data (Helm et al. 2006) to study the relationships between the genetic diversity and species richness in paper **I** and to characterise the local environmental conditions through Ellenberg indicator values in paper **II** (see section 2.3.2 for more information). For paper **III**, historical species lists were obtained from a vegetation survey conducted in 1918–1923 (Vilberg 1927). Current species lists (**III**) were compiled in 2008 and sites were additionally checked for absent species in 2009 and 2011. Species life-history traits for extinction risk analysis (**III**) were obtained from databases and additional information was extracted from literature (see Methods in paper **III** for a complete list).

Species extinction coefficient was developed to calculate the probability of local extinction for each specialist species in the analysis (**III**). We used the following formula:

$$\text{Species extinction coefficient} = \frac{(\text{number of populations gone extinct by 2011})^2}{\text{number of populations present in 1923}}$$

This equation takes into account the number of populations where a particular species has gone locally extinct and gives a greater value to those lost from more populations. This ensures that a random disappearance from one population or an unrecorded species in a single population has relatively little effect on the calculated extinction coefficient.

2.2.3. Genetic analyses

The genetic diversity analyses of *B. media* populations (**I**, **II**) were performed using isozyme vertical polyacrylamide gel electrophoresis. Isozyme variation has been shown to explain well the patterns of *B. media* genetic diversity in the landscape context (Prentice et al. 2006). *B. media* plants (25 individuals per site) were collected and grown in a greenhouse for the period of the analysis. Nine enzymes were analysed and data of seven polymorphic loci were subsequently used in the analysis: *Aat-b* (2), *Pgi-a* (4), *Skd-a* (2), *Est* (3), *Pgm* (3), *Prx* (3), *Mdh-a* (2) (the number of alleles is indicated in parenthesis). Allelic richness (the average number of alleles per loci; *A*), percentage of polymorphic loci (*%P*), gene diversity (expected heterozygosity; H_e), genetic

differentiation among populations (F_{ST}) and inbreeding coefficient (F_{IS}) were calculated. The genetic differentiation estimate was bootstrapped over loci in FSTAT (Goudet 2001) to obtain 95% confidence intervals. The effect of varying sample sizes was corrected by rarefaction method (Petit et al. 1998).

2.3. Landscape and local environmental variables

2.3.1. Landscape and human population density data

We studied the influence of landscape changes on species and population performance in all four papers. Information on landscape structure for papers **I**, **II** and **IV** was obtained from the detailed vegetation survey maps from the 1930s (1:200 000; Laasimer 1965). For paper **III,** historical data were obtained from the historical maps of G. Vilbaste (Vilberg 1927) and from the database of the Estonian Land Board in 2008 (www.maaamet.ee). Current landscape configuration was acquired from the inventory maps produced in 2000 by the Estonian Seminatural Community Conservation Association and corrected for accuracy using the most recent aerial photographs of the Estonian Land Board. To determine the influence of landscape changes on the genetic diversity of *B. media* (**I**), study sites were classified as 'stable', if they had retained about half of their habitat area, and 'unstable', if they had lost more than 90% of their former area.

Habitat connectivity was calculated using the connectivity equation (Moilanen and Nieminen 2002):

$$S_i = \Sigma \exp(-\alpha d_{ij}) A_j, \quad j \neq i,$$

where A_j is the area of patch j (ha), d_{ij} is the distance (km) between the patch centroids of i (study site) and j, and α is the parameter of exponential distribution scaling the influence of distance on migration and connectivity (average influence radius $1/\alpha$). We used α values of 0.34 (**I**, **II**) and 0.2 (**IV**) that correspond to an average migration distance of 3–5 km, which is a realistic migration range for grassland species traditionally dispersed by sheep (Bruun & Fritzbøger 2002).

Human population density, used as a proxy of human influence on plant populations (Thompson & Jones 1999) in papers **I**, **II** and **IV**, was obtained from the population censuses of Estonia. Census of 2000 (Statistics Estonia, www.stat.ee) was used for current data (people km^{-2}) and census of 1922 (Tammekann 1929) for historical data. Information from the census of 1922 was presented as a map (1:300 000) with each dot indicating 50 inhabitants (see Fig. 2 in paper **I**). Historical human population density was calculated using a modified connectivity equations (Moilanen & Nieminen 2002):

$$\text{Historical human population density} = \Sigma \exp(-\alpha d_{ij}),$$

where d_{ij} is distance (km) between habitat patch j and dot i, representing human inhabitants. α was set on 0.1, denoting average human influence to be within a radius of 10 km around a particular grassland and giving greater influence to inhabitants located closer to the grassland. Note, that similarly to the original connectivity equation, the modified formula also produces relative values without units. In paper **IV**, historical human population density in 5 km radius was taken into account and calculated by summing all dots within this radius and dividing with the circle area, thus obtaining population density values (people km^{-2}) directly comparable to current population density.

2.3.2. Environmental parameters, indicators and accompanying species

We investigated the effect of several local environmental variables on plant performance in papers **II** and **IV**. The soil depth was measured in 20 random locations at each site and soil samples for chemical analysis were collected from 5 locations and later pooled and analysed as a single sample. Soil pH (KCl method), nitrogen (Kjeldahl method) and available phosphorous content (extraction with acid ammonium lactate solution, P-AL method) were determined. Shrub cover (mainly junipers) was calculated from aerial photographs (**II**) or estimated concurrently with juniper height on site (**IV**). Ellenberg indicator values (Ellenberg et al. 1992) were used to characterise site long-term environmental conditions through the species composition of each site. Soil moisture (**II**, **IV**) and light conditions (**II**) were calculated by averaging the respective indicator values of all species recorded at a site (Wamelink et al. 2002).

Habitat specialist and generalist species richness can be used as a measure of site quality, which characterises the effects of landscape and environmental processes on the community composition and population performance (Krauss et al. 2004; Cristofoli et al. 2010; Reitalu et al. 2012). Species habitat specialization (**IV**) was estimated by combining species presence/absence data on alvar grasslands in previous studies (Helm et al. 2007; Kasari et al. 2013), their habitat requirements (Leht 2007) and distribution range in Estonia (Kukk and Kull 2005). We computed the logratio of the habitat specialist and generalist species richness in the small scale (in 10×10 cm plots) and calculated the average for the 10 m transect to characterise the processes influencing populations in the small scale, similarly to our small-scale target species abundance estimates (see section 2.2.1).

2.4. Statistical analysis

In studies **I**, **II** and **IV**, we related different landscape, human influence and environmental parameters to the response variables (genetic diversity, plant and population traits), using different model fitting methods (general linear mixed

models (**I**, **IV**) and general linear models (**II**)) and AIC (Akaike Information Criterion) based model selection techniques. Spatial correlation was taken into account in paper **I**, but was not required according to Moran's *I* autocorrelograms in the analyses for papers **II** and **IV** (tested in SAM; Rangel et al. 2010). SAS *proc mixed* procedures were used for model fitting (Littell et al. 1996) in paper **I**.

In paper **II**, models were first fitted in three sets to estimate separately the influence of 1) landscape structure, 2) environmental parameters and 3) genetic diversity on plant and population traits of *B. media*. Model averaging was used for each set of models (Burnham and Anderson 2002) and factors with greatest relative importance in each group were thus determined. These relatively most important factors from the three sets of models were subsequently combined in a variation partitioning analysis to distinguish their separate and combined effect on the selected traits. Models were fitted in SAM (Rangel et al. 2010) and variation partitioning analysis was performed in the *vegan* package (Oksanen et al. 2011) in R (R Development Core Team 2011).

To determine the influence of landscape and environmental variables on population performance, an AIC-based model selection procedure was applied in paper **IV** (*MASS* package; Venables & Ripley 2002). All explanatory variables were combined in the models in interaction with the species group ('disappearing' or 'persistent') to additionally discern the possible differences in responses of the species groups to the surrounding conditions. For best models we calculated the adjusted R^2 in the *MuMIn* package (Bartoń 2013) and additional model parameters in the *nlme* package (Pinheiro et al. 2013) to characterise the effect of factors in best models. All tests were performed in R (R Development Core Team 2013).

In order to account for the phylogenetic similarities between related species (**III**) and to avoid possible phylogenetic pseudoreplication (Tremlová & Münzbergová 2007; Bielby et al. 2010), we tested the selected life-history traits (Table 1 in study **III**) for phylogenetic signal in the *picante* package (Kembel et al. 2010) in R (R Development Core Team 2010) and used phylogenetic comparative methods in subsequent analysis in paper **III**. Phylogenetic tree for observed specialist species was obtained from the BiolFlor database (Klotz et al. 2002). Historically less abundant species were excluded if their phylogeny was unresolved. The phylogenetic tree was made ultrametric, so that the distance from the root to the tip would be the same for all species. A model was fitted, using generalized estimating equations (GEE) that consider phylogenetic relationships among species (Paradis and Claude 2002) to analyse the effects of selected life-history traits on species extinction coefficient. Model fitting and phylogenetic tree recalculation were performed in the *ape* package (Paradis et al. 2004).

3. RESULTS

3.1. The effect of landscape and local environment in determining local extinctions and population performance

Land-use and local environmental changes in northern Estonian alvars have resulted in an average loss of 29% of habitat specialist species over the last century (**III**). Seventy-one species have gone locally extinct from at least two sites since the 1920s and have an extinction coefficient above 0 (see Table S1 in Supporting Information for paper **III**). Considering the traits of the locally disappearing species, we are able to infer that the most significant drivers of local extinctions in these grasslands are decreasing site connectivity (due to loss of species that are wind-dispersed and with lower seed terminal velocity) and increasing eutrophication (loss of shorter species with preference for lower productivity; Table 1). Local extinctions taking place as a result of changes in both landscape structure and site quality give us reason to expect that both of these drivers also impact the remaining populations on the less degraded remnant grasslands.

Table 1. The effects of life-history trait values and habitat preferences on species extinction coefficient. Negative trait effect indicates a negative association between traits or habitat preferences and the extinction coefficient. Table modified from paper **III**

Trait	Trait effect (±SE)	No of obs.	*p*	*t*	*F*	d.f.	d.f.P
(1) Seed number (log)	–0.58 (±0.08)	95	***	–7.49			27.4
(2) Terminal velocity (log)	–0.75 (±0.19)	69	***	–4.01			23.1
(3) Flower duration	–0.10 (±0.06)	118		–1.79			29.3
(4) Pollen vector		112	**		7.8	2	
‘wind’;	0.02 (±0.23)			0.09			29.9
‘self-pollination’	0.39 (±0.15)		*	2.60			29.9
(5) Dispersal		98	**		6.5	2	
‘wind’	0.68 (±0.27)		*	2.52			26.8
‘other’	0.36 (±0.21)			1.76			26.8
(6) Seed weight (log)	–0.17 (±0.06)	117	**	–3.04			29.1
(7) Average plant height	–0.02 (±0.01)	97	***	–5.51			27.0
(8) Life span		121	*		4.3	1	
‘annual, biennial’	0.33 (±0.16)		*	2.08			29.6
(9) Mode of reproduction		121	*		5.0	2	
‘only by seeds or spores’	0.28 (±0.13)		*	2.18			29.6
‘mostly by seed and rarely vegetatively’	0.21 (±0.20)			1.05			29.6
(10) Seed bank		93			2.0	2	
‘transient < 1year’	–0.14 (±0.21)			–0.67			26.1
‘persistent >1 years’	0.14 (±0.17)			0.82			26.1
(11) Total seed mass per shoot (log)	–0.24 (±0.03)	93	***	–8.43			27.0
L	0.18 (±0.06)	118	**	3.23			29.3
N	–0.39 (±0.11)	109	**	–3.54			28.3

No of obs. – the number of species included into the analysis, *t* – *t*-value of the coefficient estimate, d.f.P – degrees of phylogenetic freedom. Significance levels – ***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$

The effects of specific landscape and environmental variables were more directly tested on the example of *B. media* (**II**) and six other grassland specialist species (**IV**) in the western Estonian alvars. For *B. media* the most important predictors supporting plant and population fitness on the landscape scale were historical connectivity and historical human population density (Table 1 in paper **II**). The six species in paper **IV** were most influenced by current connectivity, which was significant in all final models (Table 2; Appendix 3 in paper **IV**). Current human population density was also significant in relation to the small-scale abundance and height variation of the six species and historical human population density with positive association to plant height. Current human population density and connectivity particularly favoured the abundance of the 'disappearing' species (Appendix 3 a in paper **IV**), illustrating the higher susceptibility of these species to changes in human influence and site connectivity compared to the 'persistent' species. Several plant traits and population characteristics, like plant height (**II**, **IV**), height variation (**IV**), small-scale abundance (**IV**) and population density (**II**), displayed stronger relationships to landscape structure than to local environmental conditions.

Table 2. Plant and population traits related to landscape and environmental parameters in the best models according to AIC model selection. Table modified from paper **IV**

Landscape and human population	*t*	*p*	Environment	*t*	*p*
Abundance (Adj. R^2=0.58, d.f.=80, 4)					
historical area*species group	2.11	*	soil depth*species group	1.70	
historical area	0.53		soil depth	–0.01	
current connectivity*species group	–2.11	*	soil N content*species group	2.24	*
current connectivity	1.10		soil N content	–1.44	
current human population density*species group	–3.84	***	soil P content	–1.63	
current human population density	3.10	**	Ellenberg F	1.44	
species group	1.48		juniper height*species group	–1.41	
			juniper height	–0.10	
Plant height (Adj. R^2=0.43, d.f.=172, 4)					
current area	–3.71	***	soil depth*species group	3.30	**
historical area	–1.72		soil depth	–2.16	*
current connectivity	3.88	***	species group	–3.20	*
current human population density	2.11	*	juniper cover	3.07	**
historical human population density	3.83	***	ratio of specialist species	2.28	*
CV of plant height (Adj. R^2=0.13, d.f.=174, 4)					
current connectivity	–2.10	*	species group	–1.57	
historical connectivity*species group	2.31	*			
historical connectivity	–1.36				
current human population density*species group	–3.64	***			
current human population density	0.99				
Reproductive allocation (Adj. R^2=0.21, d.f.=168, 4)					
current area	–2.68	**	soil N content	1.89	
current connectivity*species group	–1.97	*	soil P content*species group	–1.55	
current connectivity	2.83	**	soil P content	–0.33	
species group	2.60		Ellenberg F	–2.73	**
			juniper cover	–3.02	**
			ratio of specialist species	–1.57	

Landscape and human population	*t*	*p*	Environment	*t*	*p*
CV of reproductive allocation (Adj. R^2=0.20, d.f.=167, 4)					
current connectivity	3.15	**	soil depth*species group	1.58	
historical connectivity	1.74		soil depth	–2.65	**
historical human population density*species group	-2.05	*	soil P content	1.40	
historical human population density	2.22	*	juniper height	–3.04	**
species group	1.24				

***= p <0.001, **= p <0.01, *= p <0.05

Shrub cover (mainly junipers) was the most influential environmental variable in both studies **II** and **IV**. Juniper cover ranged from 3% (paper **II**, data not shown) to 85% at the most overgrown study site (Table 2 in paper **IV**). Most of the other tested environmental variables also contributed to the models but their effect was less significant or less consistent over all computed models. Environmental factors had a more important individual or shared effect with other parameters in increasing population density, proportion of non-flowering individuals and germination success in *B. media* (**II**) and in decreasing reproductive allocation in the six species in paper **IV**.

3.2. The genetic diversity in relation to landscape structure and plant performance

The genetic differentiation between populations of *B. media* was relatively low (F_{ST} = 0.024, 95% confidence interval 0.014–0.042) and species richness in these alvar grasslands was not correlated to the genetic diversity of *B. media* (**I**). Allelic richness (*A*) and percentage of polymorphic loci (*%P*) were related to current human population density (negative effect on the genetic diversity), historical human population density and current connectivity (both affecting the genetic diversity positively; Table 1 in paper **I**). Expected heterozygosity (H_e) was not significantly related to any of the used landscape variables. Percentage of polymorphic loci exhibited a significant negative correlation with current human population density in 'unstable' grasslands (N=20; R^2=0.34; P<0.007) but not in 'stable' grasslands (N=14; R^2=0.007; P<0.784), indicating that the genetic erosion due to greater human influence has been more pronounced in patches which have lost a larger proportion of their area (Fig. 2).

The genetic diversity was used as a predictor of *B. media* population performance in paper **II**. Percentage of polymorphic loci and expected heterozygosity were most influential in the averaged models, increasing population fitness. The genetic diversity was particularly important in increasing plant potential reproductive output: *%P* explained 51% of the variation of the number of spikelets in the variation partitioning model and H_e described 10% of the CV of the number of spikelets (Fig. 3). Percentage of polymorphic loci also explained 13% of the variation in plant height and additional 7% in shared effect with shrub cover.

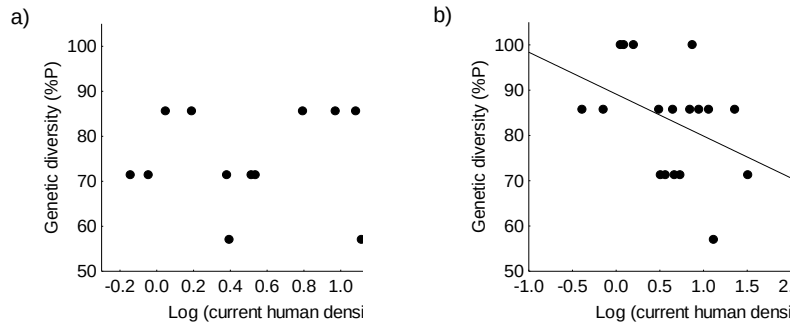

Figure 2. Percentage of polymorphic loci (*%P*) associated with current human population density in (a) 'stable' and (b) 'unstable' alvars. Figure reproduced from paper **I**

3.3. Plant and population traits indicating susceptibility to landscape changes

Nearly one third of the original specialist species richness had been lost from northern Estonian extensively fragmented alvars over the last century and several more species had lost a proportion of their local populations (**III**). Species more vulnerable to land-use changes were characterised by lighter seeds, lower seed terminal velocity, fewer seeds and lower total seed mass per shoot, self-pollination and wind-dispersal (Table 1). Extinction coefficients were also higher for short-lived and non-clonal species with lower average height, higher preference for light and lower preference for soil nitrogen content (**III**).

Prior to eventual species loss, we can expect to see changes in population and plant fitness-related traits in remnant sites with extinction debt. Our models were able to explain 20–54% of trait variation in the variation partitioning analysis of *B. media* trait responses (Fig. 3) and 13–58% of trait variation in the best models of trait responses of the six species in paper **IV** (Table 2). The number of spikelets of *B. media* and the small-scale abundance of the six species in paper **IV** were the best explained fitness and population performance traits in the studies. Species abundance patterns also showed most differences between 'disappearing' and 'persistent' species, demonstrating dissimilar responses of the two species groups to landscape changes in the western Estonian less degraded grasslands, as we expected according to their responses in the more degraded northern Estonian alvars. *B. media* potential reproductive output, as well as plant height, showed most susceptibility to loss of genetic diversity in fragmented populations, with a large amount of the trait variation determined by genetic factors (Fig. 3).

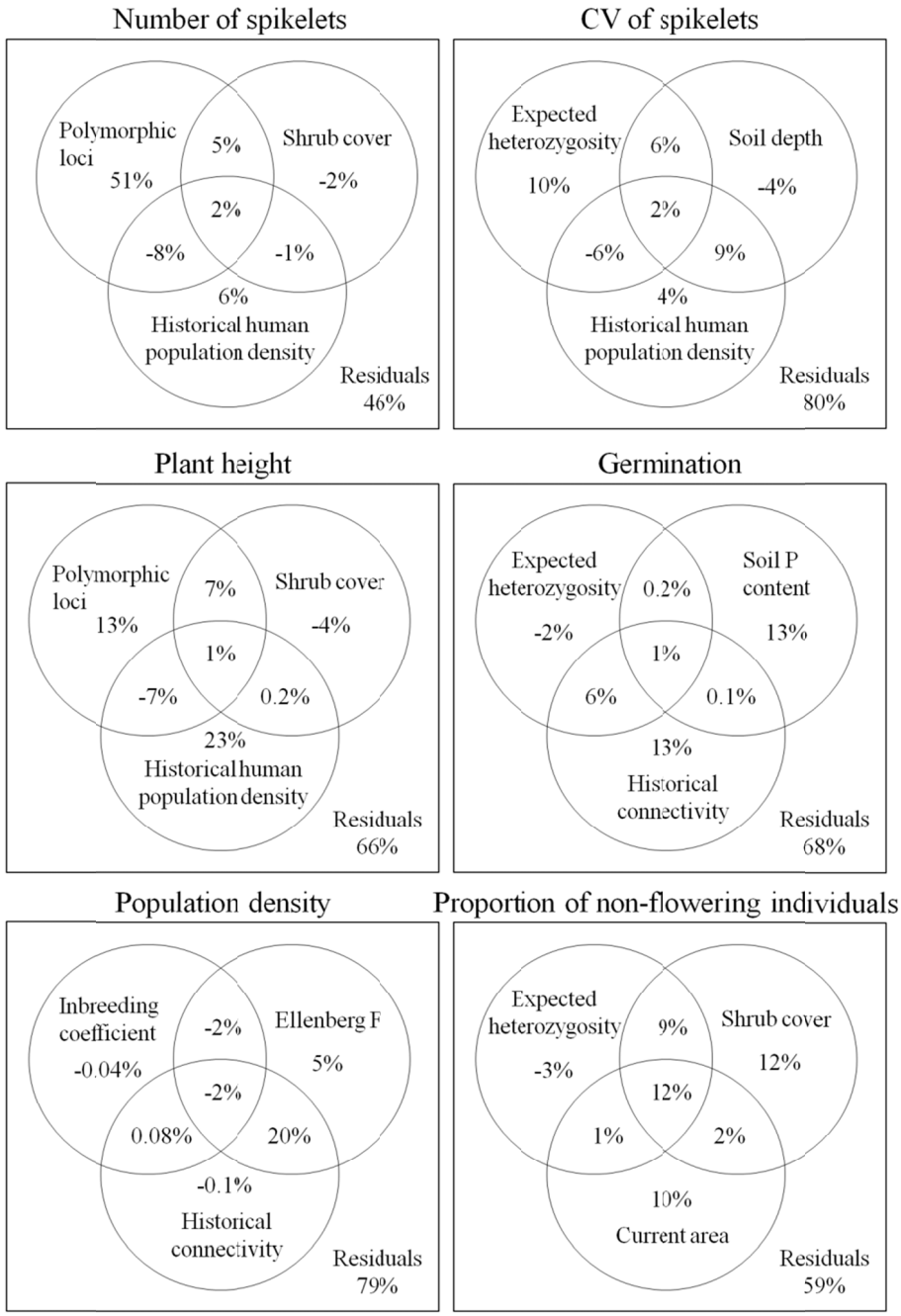

Figure 3. Plant and population characteristics of *B. media* related to the most influential genetic, landscape and environmental parameters (Table 1 in paper **II**). Diagrams show the adjusted relative influence and shared effects of the explanatory variables. Negative values indicate that the variables explain less of the model variation than any random normal variable would and the values can be interpreted as zeroes. Figure reproduced from paper **II**

Plant height and height variation were in both studies (**II**, **IV**) greatly determined by landscape factors, mainly historical and current human population density and current landscape structure, indicating the importance of historical human influence on the development of populations with higher fitness and current landscape structure in retaining the viability of these populations. Germination success of *B. media* was also to a large part determined by the positive effect of historical connectivity, including a shared variation with expected heterozygosity, indicating possible inbreeding effect in sites under long-term low connectivity conditions (Fig. 3; Table 1 in paper **II**).

In the analysis of *B. media*, environmental variables often influenced traits with a shared effect with landscape or genetic factors (Fig. 3). For instance, 20% of the variation in population density was explained by a shared variation between historical connectivity and site moisture conditions. Shrub cover and its interactions with expected heterozygosity and current area described most of the variation in the proportion of non-flowering *B. media* individuals. Juniper cover and height also affected the height and reproductive allocation patterns of the six species in paper **IV** (Table 2), indicating the significant effect of shrub encroachment, which is likely the process currently most explicitly transforming the environmental conditions at western Estonian alvar grasslands, on plant populations on these grasslands.

3.4. Time-lag in responses of plant traits and the genetic diversity

Delayed responses in species richness following habitat fragmentation have been widely recorded (Vellend et al. 2006; Gustavsson et al. 2007; Piqueray et al. 2011). We related historical landscape parameters to current genetic diversity and population performance and plant traits to test, whether similar delay can also be seen in the response of these traits (Ewers & Didham 2006; Hylander & Ehrlén 2013). Compared to species richness, which exhibits an extinction debt in these grasslands in western Estonia (Helm et al. 2006), the genetic diversity showed a quicker response to landscape changes. Historical human population density was the only significant historical parameter in the best models, coupled with current human population density and current connectivity (Table 1 in paper **I**). We also did not find a correlation between plant species richness and the genetic diversity in these sites (**I**), which highlights the different pace of these variable responses and emphasises that the expected changes in these communities are still in progress.

Plant and population traits in studies **II** and **IV** were related to both current and historical landscape structure. Population performance of the wind-pollinated *B. media* showed a stronger relationship to historical landscape (Fig. 3), whereas the six insect-pollinated species in paper **IV** were more often influenced by the current landscape (Table 2), possibly due to the more rapid response of pollinators to landscape changes (Krauss et al. 2010), which can induce changes in insect-pollinated plant populations (Biesmeijer et al. 2006; Breed et al. 2012).

4. DISCUSSION

4.1. Landscape structure and human impact in relation to population performance

Habitat loss and fragmentation have extensive effects on plant species richness and population fitness in remnant habitats (Pereira et al. 2012). In this thesis, I summarise four papers studying the effects of habitat fragmentation and degradation on plant genetic diversity, population fitness and community composition of calcareous grassland specialist species in a highly fragmented alvar grassland system in Estonia. In addition to local environmental conditions, we found strong effects of site connectivity and human influence on plant populations (**II**, **IV**). The genetic diversity of the habitat specialist *B. media* was closely related to current connectivity and human population density, as well as historical human influence (**I**). The decline of habitat specialist species richness was associated with decreasing habitat size and increasing isolation (**III**).

Good connectivity between habitat sites is essential for the long-term maintenance of viability in fragmented populations. Movement of pollen via wind or pollinators and dispersal of seeds allows gene flow between patches and enhances the genetic diversity, reduces inbreeding and thereby increases population viability (Frankham et al. 2010; Luque et al. 2012). We found both current and historical (1930s) connectivity greatly benefitting the genetic diversity (**I**), plant fitness-related traits (**II**, **IV**), population characteristics (**II**, **IV**) and specialist species persistence (**III**). Studies in the strongly fragmented but not overly degraded system of alvar grasslands in western Estonia found higher genetic diversity and populations with greater fitness in sites with grater connectivity either historically or currently (**I**, **II**, **IV**). Greater historical connectivity has driven the formation of populations with higher fitness which can still affect populations today (Frankham et al. 2010). At the same time, current connectivity is needed to retain the level of historically developed genetic diversity and to enable adaptation to changing conditions in the future (Ouborg et al. 2006).

In the more degraded northern Estonian alvars, we witnessed the consequences of connectivity loss on community composition (**III**). Nearly 30% of the original specialist species richness has been lost in these sites over the last century, responding closely to the predicted extinction debt of 40% in the western Estonian alvar grasslands (Helm et al. 2006). Species with better dispersal ability had been lost from several remnant sites, compared to those that had persisted (**III**). Most likely, the isolation of habitats had become too great for effective dispersal between the sites, which in combination with other threatening factors has led to the elimination of local populations of the more vulnerable species. Loss of good disperses has been recently detected in extensively fragmented and particularly in strongly isolated habitats, changing community composition in grasslands all over Europe (Tremlová & Münzbergová 2007; Purschke et al. 2012; Marini et al. 2012).

Human influence on fragmented habitats is strongly related to the site functional connectivity, as humans often facilitate seed and pollen transport between sites (Auffret & Cousins 2013). This mechanism has been particularly important historically, when traditional management of semi-natural habitats involved transporting livestock between different sites (Bruun & Fritzbøger 2002; Pärtel et al. 2007; Reitalu et al. 2010). Even today, moderate human influence, particularly moderate grazing, is beneficial for the species richness of semi-natural grasslands (Wagner et al. 2012), whereas overly intensive human impact reduces species richness (Thompson & Jones 1999; Pautasso 2007). Our results confirm these patterns. Greater human population density lowered the genetic diversity of *B. media* (**I**), whereas moderate human population density increased plant height (**II**, **IV**) and favoured the small-scale abundance of the 'disappearing' species (**IV**). The strong human influence was particularly harmful for the genetic diversity in the 'unstable' sites, which had lost a larger proportion of their area (Fig. 2). Populations in these 'unstable' sites have most likely been influenced by several other factors as well, such as a strong decrease in population size (Leimu et al. 2006), edge effects and altered environmental conditions (Lienert 2004), which have made them less resilient to the negative impacts of human influence. Relationships between human impact and population performance caution us to take careful measures when attending to semi-natural grasslands, which need continuous management for habitat persistence (Pärtel et al. 2005) but at the same time can suffer from too intensive human impact.

4.2. Impact of local environmental conditions on population performance

A number of factors in the surrounding environment can affect plant population performance, such as soil fertility, moisture and light conditions and different management regimes (Schaffers 2002; Klimek et al. 2007; Socher et al. 2013). Specialist plant population performance in the western Estonian alvars showed strongest association with shrub cover (**II**, **IV**). Low shrub cover can be beneficial for plant fitness, alleviating radiation and water stress (Semchenko et al. 2012), whereas greater shrub cover can cause stronger light competition and give an advantage to taller and more competitive species (Schleuning et al. 2009; Craine & Dybzinski 2013). Our results showed mainly positive effects of shrub cover and juniper height on population fitness (**II**, **IV**). Although juniper cover reached up to 85% in the most overgrown site (**IV**), this had not perceptibly reduced the fitness of our study species. However, all our selected species were rather common throughout the study system and these results should not be extrapolated to all species in these communities. Earlier studies of species richness in alvar grasslands in Sweden have found that juniper cover up to 75% increases total species richness, whereas alvar specialist species richness declined monotonically with increasing juniper cover (Rejmánek & Rosén

1988). Small-scale species richness studies in western Estonian alvars have also found a positive effect of shrub cover and light heterogeneity on total species richness (Gazol et al. 2012; Kasari et al. 2013). Generalist species have shown to benefit from increased shrub cover, while specialist species richness can also tolerate low juniper densities at small scale, resulting in an increased total number of species (Kasari et al. 2013). Moderate shade is probably most beneficial for total species richness and population fitness of several species on alvar grasslands, facilitating species with different requirements and allowing for buffering in case of varying precipitation. Nevertheless, strict specialists of open grasslands would most likely suffer from excessive juniper cover and be eliminated from strongly overgrown sites.

Northern Estonian alvars have encountered more sever degradation of local environmental conditions, including urban expansion, agriculture intensification and probable fertilisation in addition to natural juniper and pine encroachment. Species that had gone locally extinct from these grasslands (**III**) also showed susceptibility to habitat eutrophication, whereas 'persistent' species showed ability to manage higher nitrogen content and increased light competition under the changed conditions. Land-use changes and eutrophication have been identified as the main causes for species loss throughout different habitat types (Walker & Preston 2006).

Alvar grasslands all over Estonia have witnessed strong habitat loss and fragmentation. However, northern Estonian alvars have lost considerably more specialist species from individual sites than have the western Estonian alvars (**III**, Helm et al. 2006). Reasons for this difference can be attributed to stronger changes in habitat quality on the study sites and in the surrounding landscape in northern Estonia. Most of the western Estonian sites and landscape matrix around them have not been subjected to excessive human-induced degradation and can still support the persistence of many specialist species (**IV**), although a large extinction debt has been identified in this region (Helm et al. 2006). At the same time, in northern Estonia many sites are strongly eutrophic and the matrix landscape surrounding the sites is relatively hostile for alvar specialist species. Under these circumstances, habitat loss and fragmentation most likely has initially made the populations more susceptible to changes and overly intensive human influence and local habitat degradation have resulted in the final elimination of the species in northern Estonia. Avoiding these perils in western Estonian landscapes could help to preserve the currently present populations and delay the realisation of the extinction debt, although the effects of fragmentation cannot be reversed. However, it does give grounds for optimism that in western Estonia, restoring the overgrown sites and restarting traditional management could be sufficient to maintain viable populations, without the need for more extreme and expensive measures to reverse eutrophication effects, such as topsoil removal (Olsson & Ödman 2013).

4.3. Plant and population traits indicating susceptibility to landscape changes

Population characteristics and trait responses in different fragmented sites can inform us of the population condition at a particular site and of species susceptibility to landscape changes (Lienert 2004). Trait responses to habitat fragmentation have been observed in a number of plant species in different habitat types. Results, however, have been contradictory even in case of rather intuitive relationships, such as the degree of fragmentation and population size and density (e.g. Jacquemyn et al. 2002; Lienert and Fischer 2003; Adriaens et al. 2009). Disparate outcomes most likely result from differences in species life-history traits (Kolb & Lindhorst 2006), study system characteristics (Lemke et al. 2012), observed spatial scales (Bischoff et al. 2006) and other factors (Ewers & Didham 2006). Collecting more detailed information, however, can hopefully help us to elucidate some of the consequences of fragmentation and population responses to landscape changes.

In our studies, species identity and particular traits explained some differences in species response to fragmentation (**III**, **IV**). Species local extinction in northern Estonian sites was closely correlated with traits related to dispersal ability and persistence (**III**). Long-distance dispersal was impeded and anemochorous species with lighter seeds and lower terminal velocity had become locally extinct. Species with good dispersal ability can be disadvantaged in highly fragmented landscapes where site isolation is greater and dispersal related mortality is higher due to loss of diaspores in the inhospitable matrix landscape (Murphy & Lovett-Doust 2004; Riba et al. 2009; Marini et al. 2012). Additionally, trade-off between dispersal and local persistence capability through seed size can theoretically increase the vulnerability of good dispersers to local habitat degradation (Tilman et al. 1994; Bonte et al. 2012), although several studies in the natural habitats have showed the relationships to be more complex (Soons & Heil 2002; Coomes & Grubb 2003). Our results also implied that species with greater seed production were not necessarily better dispersers but rather had a competitive advantage in local persistence in more productive sites (**III**, Soons and Heil 2002). Taller plants with higher nitrogen preference and lower light requirements were also more persistent, whereas shorter species with lower productivity preference and higher light requirements were probably outcompeted in the taller vegetation under higher productivity conditions (**III**). Elimination of the less competitive and eutrophication intolerant species has been identified as a result of land-use changes in several regions with extensive human impact (Walker & Preston 2006; Van Calster et al. 2008; Wesche et al. 2012).

Study species in the western Estonian alvars also showed diverse trait responses in individual species. Some traits, such as plant height, responded rather uniformly across species (**II**, **IV**), whereas some, such as species abundance, were dependent on species characteristics (**IV**). Species small-scale abundance of the ‘disappearing’ and ‘persistent’ species responded differently

to most factors related to it, often showing contrasting relationships to landscape and environmental variables (Appendix 3 a in paper **IV**). Different responses can indicate species different susceptibility to landscape changes and to particular landscape and environmental variables. For instance, the small-scale abundance of 'disappearing' and 'persistent' species showed contrasting relationships in response to current human population density and soil nitrogen content, indicating differences in species' requirements. Current human influence favoured the 'disappearing' species, whereas higher N content benefited the 'persistent' species' small-scale abundance, illustrating the changes that can occur in species abundance and eventually in species richness at these sites, if eutrophication and lack of management should continue.

Plant height showed mostly consistent responses to tested variables across different species. In all study species, plant height, as well as height variation (**IV**) was mostly related to current and historical landscape structure (**II**, **IV**) and to a lesser extent to environmental parameters. Plant height is closely related to plant competitive ability (Berntson & Wayne 2000), potential reproductive output (Kolb 2005; Winter et al. 2008) and dispersal ability (Thomson et al. 2011). Height of *B. media* plants also showed a positive relationship with genetic diversity (**II**), indicating that the association between landscape structure and the genetic diversity could be one possible mechanism behind the relationship between plant height and landscape configuration. Environmental variables had a relatively smaller effect on plant height, although juniper cover did have a positive relationship with plant height in all study species (**II**, **IV**), most likely alleviating light and water stress (Semchenko et al. 2012) similarly in all grassland specialist species.

4.4. Delayed responses to landscape changes

Time-lag in plant and population responses to land-use changes can complicate designing conservation plans, since the effect of landscape changes and counteractive conservation measures on population fitness can manifest with a delay (Kuussaari et al. 2009). We detected relationships between population performance and historical landscape and human population structure (**I**, **II**, **IV**), indicating a certain measure of delayed response in different traits. The genetic diversity showed a stronger relationship to current human population density (**I**), whereas plant traits and population characteristics exhibited a relatively stronger association with the historical landscape factors (**II**, **IV**). The genetic diversity is often the first level of biodiversity to respond to landscape changes (Lienert & Fischer 2004; Aguilar et al. 2008), while realised trait values can take time to manifest in the phenotype.

The speed of response also depends greatly on plant life-history traits (Lindborg et al. 2012). For instance, the wind-pollinated *B. media* displayed a stronger relationship to historical landscape and human effect (**II**) than the six insect-pollinated species in paper **IV**. Increasing fragmentation of grasslands has most likely decreased pollination efficiency and induced more immediate

changes in population performance of the insect-pollinated species (Biesmeijer et al. 2006), whereas wind-pollinated plants may be able to retain their quality of pollination longer in spite of the changes in landscape structure, if local populations are sufficiently dense (Steven & Waller 2007) or there is a large source of pollen to compensate for the reduced pollen flow from other sites (Robledo-Arnuncio 2011).

Detecting a time-delay at all levels of biodiversity from genetic diversity to species richness cautions us not to overestimate the current situation of species on alvar grasslands, because most likely we can still expect considerable changes to arise even if habitat loss and continuing fragmentation cease. The time-lag can give us additional time and opportunities to execute counteractive conservation measures (Kuussaari et al. 2009) and sets an example of the slow pace that restoring the former conditions may take.

4.5. Conservation implications

Semi-natural communities are unique for their need for moderate human influence and regular management (Poschlod & WallisDeVries 2002; Pärtel et al. 2005). Results of this thesis highlight the importance of human actions for preserving the genetic diversity and population fitness, as well as species richness in anthropogenic landscapes. On the one hand, moderate management is necessary for retaining the grasslands as open habitats (**II**, **IV**), reducing the competition with taller species (**III**), creating microsites for establishment and increasing site functional connectivity (Rico et al. 2012; Wagner et al. 2012). On the other hand, overly intensive human impact and eutrophication can critically alter habitat quality and community composition at remnant sites (**III**).

Life-history traits of species that have gone locally extinct from the more degraded sites (**III**) and trait responses of the species still extant on remnant sites give us guidelines for understanding which features of landscape and local environment are most significant for population fitness and should be particularly considered when designing restoration projects and future management plans. Retaining habitat connectivity (**I**, **III**, **IV**) and moderate human impact (**I**, **IV**) are the most essential factors in the landscape scale and controlling the shrub cover and avoiding eutrophication the most important factors in the local habitat scale (**II**, **III**, **IV**). Restoring a part of the original habitat area is particularly important in unstable sites, which are more vulnerable to negative human impact due to more extensive are loss (**I**), but also in more stable sites to ensure sufficient buffer areas for plant population perseverance.

Prevention of additional eutrophication of habitats is particularly critical in the western Estonian sites, which are still relatively well preserved with regard to local environmental conditions. Habitat fragmentation has been extensive in this region (**I**, **II**, **IV**) as well as in northern Estonia and additional eutrophication could incur a rapid decline of population fitness and species richness in the western Estonian grasslands.

5. CONCLUSIONS

Severe area loss and fragmentation of Estonian alvar grasslands have caused several changes in remnant habitat condition (**I–IV**), species composition (**III**) and population fitness of extant species (**I**, **II**, **IV**). Site connectivity, moderate human population density and site juniper cover were positively related to plant and population fitness, whereas strong human influence lowered the genetic diversity of *B. media*. We found that species with good dispersal ability and sensitivity to light competition and eutrophication were most susceptible to landscape changes. Moreover, species small-scale abundance at remnant sites showed greatest difference in responses to changes in species with different susceptibility. Time-lag in trait responses to landscape changes was detected at all tested levels.

The most significant landscape-scale factors in relation to plant and population performance in western Estonian alvars were habitat connectivity and human population density, both in current and historical timescale (**I**, **II**, **IV**). The positive effect of historical and current landscape structure on plant and population performance demonstrates the importance of both historically developed viable populations and the significance of current favourable landscape structure and moderate human influence in retaining the legacy of past landscapes. Shrub cover was the most prominent environmental variable in relation to tested plant and population characteristics. Contrary to our expectations, higher juniper cover had a positive relationship with several plant and population characteristics (**II**, **IV**), most likely reflecting the stress-alleviating effect of moderate shade on grassland species.

The genetic diversity of *B. media* in the western Estonian alvars showed an association with current landscape structure, rather than to historical factors (**I**), indicating faster responses of the genetic diversity to landscape changes than the population performance of *B. media* in the same grassland system, the latter being mainly associated with historical landscape (**II**). Nevertheless, the genetic diversity was the most significant factor positively associated with the potential reproductive output of *B. media* and affected positively an important part of variation in other traits, such as plant height (**II**), indicating that the changing landscape patterns are affecting plant traits and populations are in slow transition to a new equilibrium.

Northern Estonian alvars had lost nearly 30% of the original specialist species richness in the 1920s. Declining or locally extinct species were short and short-lived species with good dispersal ability, higher light and lower productivity requirements (**III**). Traits of the ‘disappearing’ species indicated that the main factors exacerbating specialist species populations in remnant alvar grasslands are increasing functional isolation, which hinders seed dispersal between habitat fragments, and eutrophication, which benefits species with higher nutrient requirements and better competitive ability through increased light competition (**III**). Trait responses of the ‘disappearing’ and ‘persistent’ species in the western Estonian grasslands revealed that plant height responded

quite uniformly to landscape changes in all species, whereas the species abundance showed contrasting relationships among species groups (**IV**). The small-scale abundance of the 'disappearing' species had a positive association with moderate current human influence and a negative relationship with soil nitrogen content. The 'disappearing' species thus exhibit sensitivity to moderate human influence and the impact of eutrophication even in these relatively well preserved western Estonian grasslands.

We detected signs of a delayed response to landscape changes at all tested levels. The genetic diversity (**I**), plant trait responses and population characteristics (**II**, **IV**) all exhibited some level of association with historical landscape rather than to the current. The genetic diversity showed the fastest response (**I**), even though plant and population traits of *B.* media retained their association with historical factors (**II**). All studied populations appeared to be in a state of transition and becoming slowly more in accordance with the current landscape structure. Recognising that the characteristics of populations, which we currently observe on sites are not the equilibrium state of populations but a phase of transition set to motion by past landscape changes, cautions us not to take the current state for granted and to account for the imminent changes in populations when planning conservation measures.

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SUMMARY IN ESTONIAN

Muutused taimede liigirikkuses ja populatsioonide seisundis vastusena elupaikade kaole ja killustumisele

Inimtegevusest põhjustatud elupaikade kadu ja killustumine on üks olulisemaid elurikkust ohustavaid tegureid kogu maailmas. Euroopa pool-looduslikud niidud on viimase sajandi jooksul kaotanud suure osa oma kunagisest pindalast nii põllumajanduse intensiivistumise, linnastumise kui traditsioonilise majandamise lakkamise tõttu. Näiteks Eesti loopealsed on kaotanud rohkem kui 70% oma kunagisest pindalast. Elupaikade killustumise tagajärjel kahanevad paljude liikide populatsioonid ning muutuvad maastikus isoleeritumaks. Väikesed populatsioonid on aga palju tundlikumad väliskeskkonna muutustele ning juhuslikele populatsiooni suuruse kõikumistele. Samuti ohustab väikesi populatsioone geneetilise mitmekesisuse vähenemine ja sellest tingitud populatsioonide elujõulisuse langus.

Elupaikade killustumise tagajärjel võivad mitmed liigid kooslustest kaduda, kuna muutunud maastikustruktuur ja keskkonnatingimused ei ole nende pikaajaliseks püsimiseks enam sobilikud. Muutustele reageerimine võib aga võtta aastakümneid või isegi aastasadu, sest mõnda aega suudavad taimepopulatsioonid vastu pidada ka tingimustes, mis nende pikaajalist püsimajäämist ei toeta. Sellist nähtust, kui kooslustes esinevad liigid, mis pikas perspektiivis võivad sealt kaduda, nimetatakse väljasuremisvõlaks. Lääne-Eesti loopealseid uurides on leitud, et viimase sajandi jooksul toimunud maastikumuutuste tõttu on neil kujunenud arvestatav liigivõlg ning aja jooksul võivad need kooslused kaotada kuni 40% praegustest elupaigaspetsiifilistest liikidest.

Taimeliikide tunnused võimaldavad hinnata liikide vastuvõtlikkust maastikumuutustele ning nende tõenäosust lokaalselt kooslustest kaduda. Killustunud kooslustes võiks näiteks hea levimisvõime anda liikidele eelise püsimajäämiseks. Kui aga elupaik satub liiga tugevasse isolatsiooni, siis võivad hea levimisvõimega liigid hakata hoopis kaduma, kuna suur osa nende seemnetest satub ebasobivatesse kasvukohtadesse. Muutuvate keskkonnatingimuste korral on sageli eelistatud pikaealised, klonaalsed ja tugevama konkurentsivõimega liigid, kuigi on leitud ka klonaalsete liikide osakaalu vähenemist nendes kooslustes, kus suuremad muutused on toimunud juba mitmete sajandite vältel.

Enne liikide lõplikku kadumist kooslustest võivad taimede tunnused anda märku populatsioonis toimuvatest muutustest. Muutused taimede fenotüübis vastusena maastikustruktuuri ja elupaiga tingimuste muutustele võivad olla vägagi varieeruvad, sõltuvalt näiteks liigi elukäigu tunnustest. Samuti võivad populatsioonide omadustes ning isendite fenotüübis toimuvad muutused olla ajalise viibega, sarnaselt taimeliikide kadumisele kooslustest. Ajaline nihe nii liigilise mitmekesisuse vähenemisel kui populatsioonide elujõulisuse muutumisel raskendavad koosluste ja populatsioonide tegeliku seisundi hindamist ning muudab keerukamaks adekvaatsete looduskaitseliste otsuste tegemise.

Käesolevas töös uurisin Eesti loopealsetel toimunud maastikumuutuste mõju loopealsetele karakteersete liikide tunnustele ning populatsioonide omadustele. Uuritud loopealsete pindala erinevates Eesti piirkondades oli kahanenud 80–90% võrra. Samas on Põhja-Eesti loopealsed on olnud pikka aega tugeva inimmõju all ning keskkonnatingimused on mitmetel aladel tugevalt degradeerunud linnastumise, põllumajanduse intensiivistumine või karjääride loomise tagajärjel. Lääne-Eesti saartel asuvad looalad on peamisel kahanenud metsastamise tagajärjel ning kuigi senini säilinud jäänukkooslused on suures osas kadakatega kinni kasvamas, on keskkonnatingimused neil siiski looliikide püsimiseks soodsamad kui Põhja-Eesti niitudel.

Töös selgitasin, kuidas on viimase sajandi jooksul toimunud maastikumuutused mõjutanud niiduspetsialistist kõrrelise, keskmise väriheina (*Briza media* L.) geneetilist mitmekesisust (**I**) ning populatsioonide seisukorda (**II**). Seejärel määrasime kindlaks, millised liigid on 85 aasta vältel kadunud Põhja-Eesti tugevasti degradeerunud loopealsetelt (**III**) ning võrdlesime, kas Põhja-Eesti alvaritel registreeritud 'kaduvad' ning 'püsivad' liigid reageerivad erinevalt ka Saaremaa ja Muhu vähem degradeerunud loodudel toimunud muutustele (**IV**). Meie eesmärgiks oli teada saada:

1) millised maastiku- ja keskkonnafaktorid on kõige olulisemad liikide ja populatsioonide seisundi määramisel (**I**–**IV**);
2) millised maastiku ja keskkonna parameetrid mõjutavad kõige enam keskmise väriheina geneetilist mitmekesisust (**I**) ning milline on geneetilise mitmekesisuse roll populatsiooni seisundi määramisel (**II**);
3) millised elukäigu tunnused ning tunnuste reaktsioonid näitavad liikide vastuvõtlikkust maastikumuutustele (**II**, **III**, **IV**);
4) kas geneetiline mitmekesisus, taimede ning populatsioonide tunnused reageerivad maastikumuutustele ajalise viibega (**I**, **II**, **IV**).

Kõigi väitekirja kaasatud tööde tulemused kinnitasid, et olulisimad taimede tunnuseid mõjutavad faktorid maastikuskaalas on elupaikade sidusus (**I**–**IV**) ning inimmõju tugevus (**I**, **II**, **IV**). Elupaikade sidusus on vajalik võimaldamaks koosluselaikude vahel õietolmu liikumist ja seemnete levimist, mõjutades seeläbi geneetilise mitmekesisuse säilimist ning populatsioonide elujõulisust. Seemnelevi elupaigalaikude vahel aitab kaasa ka liigirikkuse kujunemisele ning vähendab populatsioonide riski lokaalselt kaduda. Ajalooliselt kujunenud liigirikkuse mustrid ning geneetiline mitmekesisus võivad maastikumuutuste järel olla veel pikka aega jälgitavad. Tänane sidusus on aga oluline ajalooliselt kujunenud mitmekesisuse säilimiseks tänastes killustunud maastikes.

Inimeste asustustihedus on heaks inimmõju mõõduks maastikuskaalas. Eriti oluline on inimeste roll pool-looduslikes kooslustes, mis on ajalooliselt kujunenud ja saavad avatuna püsida vaid mõõduka inimmõju toel. Traditsioonilised pool-looduslike koosluste majandamisvõtted hõlbustasid taimede seemnelevi koos loomakarjade liikumise ning heinaveoga. Mõõdukas inimmõju võib ka tänapäeval teatud määral samu funktsioone täita, kuid liigne inimasustuse tihedus ja sellega kaasnevad tegurid kahandavad pool-looduslike elupaikade kvaliteeti ning vähendavad liigirikkust.

Meie tulemused näitasid veenvalt maastikustruktuuri ja mõõduka inimmõju olulisust Eesti lookooslustele. Keskmise väriheina geneetiline mitmekesisus oli positiivselt seotud tänase elupaikade sidususe ning ajaloolise inimasustuse tihedusega (**I**). Väriheina isendite ja populatsioonide kohasus olid positiivselt seotud ajaloolise inimasustuse ning sidususega (**II**), käsikirjas **IV** uuritud kuue liigi tunnuste puhul oli läbivalt oluline tänane sidusus. Tugev kaasaegne inimmõju vähendas keskmise väriheina geneetilist mitmekesisust (**I**), mõõdukas inimasustuse tihedus aga soodustas 'kaduvate' liikide ohtrust Lääne-Eesti loopealsetel (**IV**). Ka Põhja-Eesti tugevas isolatsioonis olevatelt loodudelt olid kadunud mitmed hea levimisvõimega liigid, mis viitab aladevahelise sidususe olulisele panusele liikide lokaalsele püsimisele (**III**).

Keskkonnatingimustest oli populatsioonide seisundi määramisel kõige olulisem kadakate katvus (**II**, **IV**). Loodude kinnikasvamine kadakatega on üks olulisemaid ohutegureid Lääne-Eesti loopealsetel. Kadakate katvus uurimisaladel varieerus 3–85% vahel. Varasemad tulemused on näidanud, et mõõdukas, kuni 30% kadakate katvus ei oma looliikidele olulist negatiivset mõju, samas kui kõrgem katvus võib soodustada mitte-loospetsiifiliste liikide sisenemist kooslusesse ning halvendada tingimusi looliikide jaoks. Meie tulemused ei näidanud kadakate selget negatiivset mõju looliikide populatsioonidele (**II**, **IV**) ning pigem oli kadakatel teatav soodne mõju uuritud taimede tunnustele. Samas tuleb rõhutada, et kõik antud töös uuritud liigid olid suhteliselt sagedased looliigid ning kadakate mõju haruldasematele liikidele võib erineda meie tulemustest.

Põhja-Eesti loopealsed olid viimase sajandi jooksul kaotanud keskmiselt ligi 30% oma kunagisest liigirikkusest (**III**). See number on väga lähedane ennustatud 40% suurusele väljasuremisvõlale Lääne-Eesti loopealsetel, mis näitab, et tõenäoliselt on Põhja-Eesti alvarid juba suure osa oma väljasuremisvõlast 'maksnud'. Uurimisaladelt täielikult või osaliselt kadunud (nö 'kaduvate') liikide tunnuste analüüs näitas, et maastikumuutustele ja keskkonna degradeerumisele tundlikumad olid liigid, millel olid kergemad ja lenduvamad seemned, mille isendid on madalamakasvulised, eelistavad kasvada paremates valgustingimustes ning madalama toitainetesisaldusega keskkonnas (**III**). Seega olid kadunud hea levimisvõimega liigid, mis ei suuda hakkama saada kõrge produktiivsuse ja tugeva valguskonkurentsi tingimustes. Põhja-Eesti loopealsed on kohati tugevalt eutrofeerunud ning kõrgema produktiivsusega kui Lääne-Eesti alvarid. See keskkonnatingimuste erinevus võib ka selgitada, miks võrreldava ulatusega elupaikade killustumise tagajärjel on Eesti läänesaarte looalad tunduvalt liigirikkamad kui Põhja-Eesti loopealsed ning viitab potentsiaalselt kiiretele muutustele liigirikkuses, mida koosluste eutrofeerumine võib kaasa tuua ka hetkel heas seisukorras loopealsetel.

Liikide tunnuste reaktsioonid maastikumuutustele sõltuvad oluliselt liikide elukäigu tunnustest (**IV**). Näiteks eri liiki taimede kõrgus reageeris muutunud tingimustele suhteliselt ühetemoodi. Samas liikide väikseskaalaline ohtrus aladel sõltus sellest, kas tegu oli 'kaduva' või 'püsiva' liigiga. Tänane tihedam inimasustus soodustas 'kaduvate' liikide ohtrust, kõrgem lämmastikusisaldus

mullas aga vähendas seda. 'Püsivad' liigid reageerisid neile parameetritele vastupidiselt – kõrgem lämmastiku sisaldus mullas andis neile liikidele eelise, samas kui tänane tugevam inimmõju vähendas nende väikeseskaalalist ohtrust (**IV**). Vastandlik reageerimine eri faktoritele liigi ohtruses näitab, et ka suhteliselt hästi säilinud Lääne-Eesti loopealsetel on juba näha teatud erinevused 'kaduvate' ja 'püsivate' liikide populatsioonides ning need erinevused võivad aja jooksul süveneda.

Ajaline nihe tunnuste reageerimisel maastikumuutustele oli märgatav enamike uuritud tunnuste puhul (**I**, **II**, **IV**). Keskmise väriheina geneetiline mitmekesisus oli küll suurel määral seotud tänase maastikuga, kuid ka ajaloolise inimmõju efekt oli veel märgatav (**I**). Samas olid väriheina isendite fenotüübilised ja populatsiooni tunnused alles lähemalt seotud ajaloolise maastikuga ning tunduvalt vähem tänasega (**II**). Kuue uuritud 'kaduva' ja 'püsiva' liigi tunnused olid seotud nii ajaloolise kui tänase maastikuga, seejuures tänane maastik omas teatud määral tugevamat mõju (**IV**). Võimalik, et nende kuue liigi tunnuste kiirem reaktsioon maastikumuutustele võrreldes keskmise väriheinaga on seotud sellega, et need liigid on kõik putuktolmlejad (**IV**), samas kui värihein on tuultolmleja (**II**). Elupaikade killustumine mõjutab tolmeldajate liigirikkust, ohtrust ja tolmeldamise efektiivsust ning võib seega tingida putuktolmlejate liikide kiirema vastuse maastikumuutustele.

Pool-looduslikud kooslused on unikaalsed elupaigad, mis vajavad säilimiseks mõõdukat majandamist, kuid liiga tugev inimmõju võib rikkuda nende koosluste tasakaalu ja vähendada elurikkust. Käesoleva töö tulemused kinnitasid, et loospetsiifiliste liikide säilimiseks on oluline tagada piisav aladevaheline sidusus (**I**–**IV**) ja mõõdukas inimmõju (**I**, **IV**), takistada eutrofeerumist (**III**, **IV**) ning reguleerida kadakate katvust (**II**, **IV**). Lisaks on äärmiselt oluline looduskaitseliste otsuste tegemisel arvestada sellega, et praegune näiv taimepopulatsioonide seisund ei ole pikaajaliselt stabiilne olukord, vaid iseloomustab hetkel käimasolevaid muutusi, mille käivitasid aastakümnete tagused maastikuprotsessid ning mille lõpptulemust on praegusel hetkel raske ette ennustada (**I**, **II**, **IV**).

ACKNOWLEDGEMENTS

My deepest gratitude goes to my supervisors Aveliina Helm and Meelis Pärtel for your guidance, advice, patience, most kind support and all the opportunities you have provided me with. I particularly thank Aveliina for always being there for me (in spite of the fact that I most inconveniently always tend to submit and defend my theses when you are having a baby). You have been the best supervisor I could ever wish for!

I thank all my co-PhD students in the Macroecology workgroup for invigorating discussions, memorable fieldwork, and best company there is – particularly Liina, Riin, Liis, Marge, Kersti, Rita, Ene and Inga. Special thanks go to Liina – it has been great working with you both in the field of science as well as in science education. I am grateful to Robert for all the help you have provided and our foreign post-docs and researchers – Antonio, Jesse, Jodi, Rob and Jon – for introducing me different approaches to science. I thank all my co-authors, advisors in manuscript preparation and field work. Special thanks to Riin, Liina and Elen for comments on my thesis manuscript and Kai for her help with proof-reading.

I thank my family for their support and not too many objections to my decision to become a 'flower sniffer' (i.e. plant ecologist). I am especially grateful to my mom for always having the time and patience and interesting insights to share with me. I thank Eero for your patience with me and for understanding, why I had to leave every Sunday evening. My deep gratitude also goes to my former biology teacher Inge Vahter, who first brought me to biology and kindled my interest for doing scientific research. Every time I finish a paper, supervise a student or give a presentation I think of you. Thanks to all my friends, each and every one of you, for your share in my life and for getting me out of the office every now and then. I am most truly grateful to my lifelong best friend Elen for being my glue when I happen to be broken and for simply being there for me. Always. One can't also underestimate the effect of good music and literature that sometimes offer alternative hypotheses to life, universe and scientific research, such as "Always take into consideration that you might be dead wrong" or "Things just happen. What the hell" (T. Pratchett).

***

This study was funded by Estonian Science Foundation (grants no. 7610, 6614, 6619, 7544 and 8323), Estonian Research Council (grants no. 9223 and 8613), targeted financing (SF0180095s08), European Union through the European Regional Development Fund (Centre of Excellence FIBIR), European Commission 6th Framework Programme via the project COCONUT (SSPI-CT-2006-044346), and FP 7 via the project STEP (EU FP7 244090-STEP-CP-FP).

PUBLICATIONS

CURRICULUM VITAE

Name: Krista Takkis
Date of birth: 4.02.1986
Citizenship: Estonian
Address: Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, Tartu 51005, Estonia
Phone: +372 5812 1294
E-mail: krista.takkis@ut.ee

Current position:
Institute of Ecology and Earth Sciences, University of Tartu, PhD student

Education:

2009– present	University of Tartu, PhD candidate in botany and ecology
2007–2009	University of Tartu, MSc in biology
2004–2007	University of Tartu, BSc in biology
1992–2004	Saaremaa's Co-ed. Gymnasium

Language skills:
Estonian (mother tongue)
English (proficient user)
German (independent user)
Russian (basic user)
Livonian (basic user)

Institution and position held:

2008–2013	University of Tartu, laboratory and field work assistant
2012, 2013, 2014	Tartu Environmental Education Centre, co-organiser of the Estonian Biology Olympiad for secondary school
2011–2012	Archimedes Foundation, student research project supervisor
2010	Estonian University of Life Sciences, field work assistant
2007	University of Tartu, field work and laboratory assistant
2004, 2005	Saaremaa's Co-ed. Gymnasium, co-supervisor of botany field courses

Research interests:
Effects of landscape fragmentation, landscape history and environmental changes on plant species richness and population fitness, trait responses of common species to landscape changes, landscape genetics and dry calcareous semi-natural grasslands.

Publications:

Takkis, K., Saar, L., Pärtel, M., Helm, A. The role of environmental and landscape factors in determining plant abundance and fitness-related traits in six specialist plant species in fragmented grasslands. *Manuscript*.

Dallimer, M., Jacobsen, J.B., Lundhede, T.H., **Takkis, K**., Giergiczny, M., Thorsen, B.J. Patriotic values for public goods: transnational trade-offs for biodiversity and ecosystem services. *Manuscrtipt*.

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Conference presentations:

Takkis, K., Saar, L., Pärtel, M., Helm, A. Disappearing and persistent species in fragmented grasslands: different responses to landscape and environmental changes indicate susceptibility to future extinctions. *Oral presentation*. 26th Conference of the Plant Population Biology Section of the Ecological Society of Germany, Austria and Switzerland (GfÖ). 09.–11.05. 2013, Tartu, Estonia.

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of the Ecological Society of Germany, Austria and Switzerland (GfÖ) 2010. 30.08.–03.09.2010, Giessen, Germany.

Takkis, K., Helm, A., Saar, L., Pärtel, M. Population fitness of habitat specialist grass in declining habitats. *Poster presentation*. Baltic Botany XXIII Conference-Expedition. 19.–22.07.2010, Haapsalu, Estonia.

Takkis, K., Saar, L., Helm, A., Pärtel, M. Contrasting responses of two grassland species to habitat fragmentation. *Poster presentation.* International Association for Vegetation Science (IAVS) 52th Symposium. 30.05.–03.06. 2009, Chania, Greece.

Awards and scholarships:

2011, 2012 Doctoral school of Earth Sciences and Ecology, travel grants

2009, 2011 Archimedes Foundation, travel grants

2007 Saaremaa Local Governments Association, Johann von Luce Scholarship

Other activities and membership:

2013 Co-organiser of the pre-excursion ("West-Estonia and the Islands") of the 56th Symposium of the International Association for Vegetation Science (IAVS), 20.–25.06.2013

2010 Co-organiser of the Biodiversity Day of the GEO international magazine in Tartu, Estonia

2007–present Member of the Tartu Students' Nature Conservation Circle, member of the board in 2008/09

Courses attended:

2012 Graduate course "Issues in Diversity" (lecturer Prof. Susan Harrison, University of California, Davis, USA), 03.–07.09.2012, University of Oulu, Finland

ELULOOKIRJELDUS

Nimi: Krista Takkis
Sünniaeg: 4.02.1986
Kodakondsus: eestlane
Aadress: Tartu Ülikool, Ökoloogia ja maateaduste instituut, botaanika osakond, Lai 40, 51005 Tartu, Eesti
Telefon: +372 5812 1294
E-post: krista.takkis@ut.ee

Praegune töökoht:
Tartu Ülikool, Ökoloogia ja maateaduste instituut, botaanika osakond, doktorant

Haridus:

2009–	Tartu Ülikool, botaanika ja ökoloogia doktorantuur
2007–2009	Tartu Ülikool, botaanika ja mükoloogia eriala magistrikraad
2004–2007	Tartu Ülikool, botaanika ja mükoloogia bakalaureusekraad
1992–2004	Saaremaa Ühisgümnaasium

Keelteoskus:
eesti keel (emakeel)
inglise keel (suurepärane)
saksa keel (hea)
vene keel (baasteadmised)
liivi keel (baasteadmised)

Töökogemus:

2008–2013	Tartu Ülikool, preparaator
2012, 2013, 2014	Tartu Keskkonnahariduse Keskus, Eesti Bioloogiaolümpiaadi põhikoolivooru kaaskorraldaja
2011–2012	SA Archimedes, õpilasuurimuse juhendaja
2010	Eesti Maaülikool, välitööde teostaja
2007	Tartu Ülikool, preparaator
2004, 2005	Saaremaa Ühisgümnaasium, välipraktikumi kaasjuhendaja

Peamised uurimisvaldkonnad:
Maastike killustumise, maastikuajaloo ja keskkonnatingimuste muutuste mõju taimede liigirikkusele ja populatsioonide kohasusele, tavaliste taimede tunnuste reageerimine maastikumuutustele, maastikugeneetika, kuivad lubjarikkad poollooduslikud kooslused.

Publikatsioonid:
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Saadud uurimistoetused ja stipendiumid:

2011, 2012 Maateaduste ja ökoloogia doktorikooli välissõidutoetused

2009, 2011 SA Archimedese Kristjan Jaagu ja DoRa programmide sõidu-toetused

2007 Saaremaa Omavalitsuste Liidu Johann von Luce nimeline stipendium

Muu teaduslik organisatsiooniline ja erialane tegevus:

2013 Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) 56. sümpoosioni eelekskursiooni ("Lääne-Eesti ja saared") kaaskorraldaja, 20.–25.06.2013

2010 Rahvusvahelise GEO ajakirja Elurikkuse päeva kaaskorraldaja, 14.–15.05.2010, Tartu, Eesti

2007– Tartu Üliõpilaste Looduskaitsering, s.h 2008/09 juhatuse liige

Erialane enesetäiendus:

2012 Kursus "Issues in Diversity" (lektor prof. Susan Harrison, University of California, Davis, USA), 03.–07.09.2012, Oulu Ülikool, Soome

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